

TWO NEW SPECIES OF *CENTROLENELLA*
(ANURA: CENTROLENIDAE) FROM
NORTHWESTERN PERU

John E. Cadle and Roy W. McDiarmid

Abstract. — Two new species of *Centrolenella* are described from the Pacific versant of the Andes in northern Peru (Río Zaña, Cajamarca Department). These constitute the first records for the genus on the western slopes of the Andes in Peru. *Centrolenella euhystrix*, a large species (males to 31.3 mm, females to 33.6 mm snout–vent length), has a distinctive coloration (dark greenish black when active at night), broad digits, and large hands. Males of this species have very spinose dorsal skin and lack humeral spines. Although males of *C. euhystrix* call from rock ledges in or along cascading streams, an unusual calling site for *Centrolenella*, neither egg masses nor reproduction were observed in this species. *Centrolenella hesperia* is a smaller species (males to 27.3 mm, females to 28.8 mm snout–vent length) which lacks a tympanum, is bright green when active, and has a distinctive lateral white stripe from the snout to the groin. Males of this species have spinose dorsal skin and humeral spines. The reproductive behavior, vocalizations, and larval morphology of *C. hesperia* are similar to those known for other species of *Centrolenella* except that females have an unusual behavior at the clutch and egg masses contain empty capsules. The intercalary elements in these species are mineralized; the nature of this element in the Centrolenidae and other frogs is discussed.

Resumen. — Se describen dos nuevas especies de *Centrolenella* de la vertiente pacífica de los Andes en el norte del Perú (Río Zaña, Departamento de Cajamarca). Estas especies se componen el primer registro del género en Perú occidental. *Centrolenella euhystrix* es una especie grande (los machos alcanzan a 31.3 mm de longitud corporal y las hembras a 33.6 mm) que tiene una coloración distintiva (negro verdoso oscuro durante la actividad nocturnal), los dedos anchos, y las manos grandes. Los machos de esta especie son muy espinosos y carecen de espinas humerales. Aunque los machos de *C. euhystrix* cantan desde anaqueles rocosos en torrentes, o a lo largo de los mismos, un sitio de canto poco frecuente para *Centrolenella*, ni masas de huevos ni la reproducción fueron observadas en esta especie. *Centrolenella hesperia* es una especie más pequeña (machos hasta 27.3 mm de longitud corporal, hembras hasta 28.8 mm) que carece de un tímpano, es verde brillante cuando está activa, y tiene una raya lateral blanca desde el hocico hasta la ingle. Los machos de esta especie son también espinosos y tienen espinas humerales. El comportamiento reproductivo, las vocalizaciones, y la morfología larval de *C. hesperia* son similares a aquellas conocidas de otras especies de *Centrolenella*, menos que las hembras muestran un comportamiento extraña a la nidada, y que las masas de huevos contienen cápsulas vacías. Los elementos intercalares de estas especies están mineralizados; se discute la forma de este elemento en las Centrolenidae y otras ranas.



Fig. 1. Map of the central Andes of southern Ecuador and northern Peru showing the Monte Seco area (star), the type locality for *Centrolenella euhystrix* and *C. hesperia*, and all other localities (dots) at which species of *Centrolenella* are known to occur. The light hatching indicates areas between 1000 m and 3000 m; darker areas indicate those regions above 3000 m. The Huancabamba Depression of northern Peru and southern Ecuador has only a few, disjunct areas above 3000 m.

Many frogs of the genus *Centrolenella* (Centrolenidae) are known from the eastern Andean slopes of Colombia, Ecuador, and Peru (Frost 1985), and new species are being discovered at an astonishing rate (Duellman & Burrowes 1989; Flores 1985, 1987; Flores & McDiarmid 1989). Cannatella & Duellman (1982) noted 10 species in Peru (nine discovered since the mid-1970s), and indicated five undescribed species from the Amazonian slopes. Although *Centrolenella* is known from the western foothills and slopes of the Andes in Colombia and Ecuador, none has been reported from Peru's western slopes. Herein we describe two species from the Pacific versant of northern

Peru about 350 km south of the nearest reported localities on the Pacific versant in Ecuador, and about 175 km southwest of the nearest reported locality (Cannatella & Duellman 1982) on the Amazonian versant of Peru (Fig. 1).

Cadle collected during the periods 1 May to 25 June, 1987 and 13 to 31 January, 1989, near Monte Seco, a coffee cooperative at 1200 m in the valley of the Río Zaña, Department of Cajamarca, Peru (Fig. 2). Although the coast and western slopes of the Peruvian Andes are generally arid and support primarily desert or dry scrub forest, local conditions sometimes permit more mesic environments, particularly in northern Peru (Koepcke 1961). The slopes north and east of Monte Seco above about 1500 m support a wet forest that receives heavy rains from January to April, and that is enveloped by dense clouds for at least the early part of the dry season (May to December). Frogs were collected near streams and waterfalls whose headwaters originate on a ridge north and east of Monte Seco. Locally, the highest mountains extend to about 3000 m elevation.

Methods and Materials

Using dial calipers, we measured to the nearest 0.1 mm as follows: snout-vent length (SVL), straight line from tip of head to vent; head length (HL), angle of the jaw to tip of the head; head width (HW), width of the head at the angle of the jaw; snout length (SL), anterior border of eye to tip of head; eye diameter (ED), measured in the horizontal plane; eye to nostril (EN), anterior border of eye to middle of the nostril; tympanum width (TW), measured in horizontal plane; tibia length (TL), measured with the limb flexed; hand length (HnL), from the proximal border of the outer palmar tubercle to tip of digit III. Webbing formula notations follow Savage & Heyer (1967), as modified by Myers & Duellman (1982). In determining webbing formulae, we used the point of intersection of the web base with a

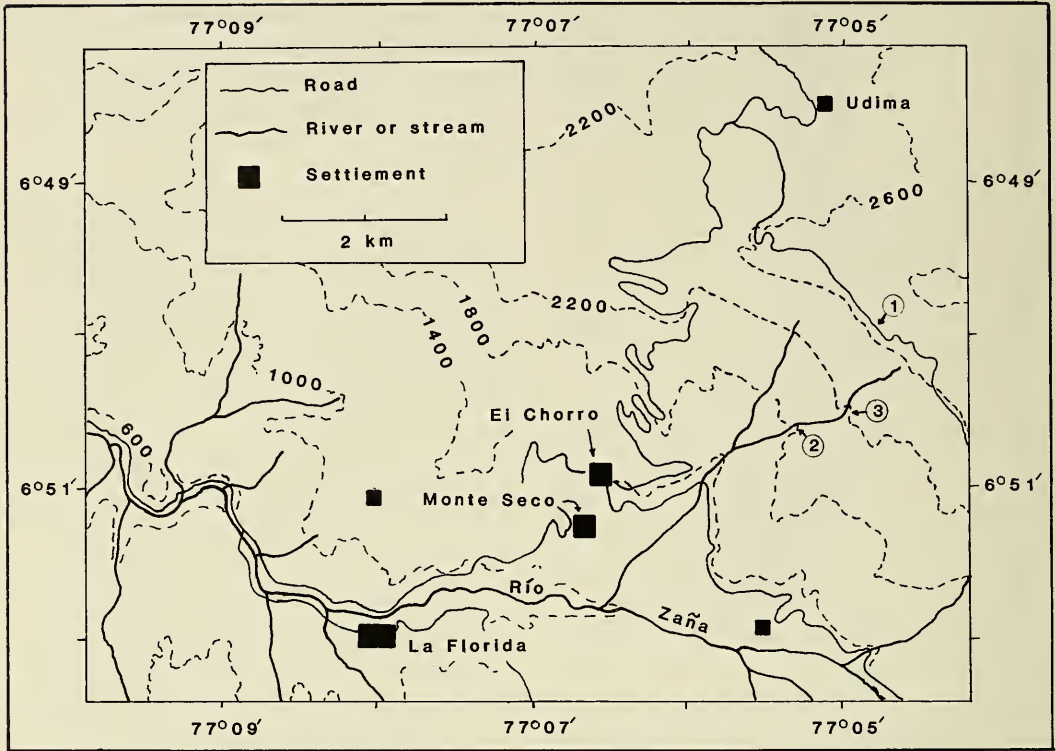


Fig. 2. Map of the Monte Seco region showing type localities and local place-names. Numbered sites refer to the following: (1) Type locality for *Centrolenella euhystrix*; (2) Type locality for *Centrolenella hesperia*; (3) "Chorro Blanco"—a waterfall and local landmark. Cadle's field camps were near site 2. Contours are in meters.

perpendicular drawn to the digit at that point. Digit lengths were determined as the relative extent of digit protrusion from the hand or foot. Nuptial pads were classified according to Flores (1985). Developmental stages follow Gosner (1960), and tadpole terminology follows Altig (1970).

We recorded calls of one species with a SONY ECM-929LT microphone and Walkman Professional® cassette tape recorder. A copy of the tape has been deposited in the tape archive, Division of Amphibians and Reptiles, National Museum of Natural History. These calls were analyzed using a Kay Digital Sona-Graph 7800 and a Multigon Uniscan II real-time analyzer. Pulse rates and call lengths were measured from waveform analyses or from wide-band audiospectrograms. Call rates were measured from the real-time analyzer screen.

Two specimens cleared and double-stained for cartilage and bone using the method of Dingerkus & Uhler (1977) were used for osteological descriptions. Museum depositories for specimens are abbreviated as in Leviton et al. (1985), except for the museum formerly known as the Museo de Historia Natural "Javier Prado" (MHNJP) in Lima, Peru. This museum, presently known as the Museo de Historia Natural de San Marcos, is abbreviated as MHNSM.

Descriptions

Centrolenella euhystrix, new species Figs. 3–5

Holotype.—Field Museum of Natural History (FMNH) 232510 (field number J. E. Cadle 7628), an adult male, taken from the ridge above basecamp (near Chorro

Blanco), about 4–4.5 km (airline) NE of Monte Seco, Río Zaña, Department of Cajamarca, Peru, 2610 m. (Fig. 2). Collected 16 May 1987 by J. E. Cadle.

Paratypes.—Fifteen specimens with the following data: FMNH 232509 (adult male), 232511 (adult male, cleared and stained), 232513–14 (adult male and female respectively), and MHNSM 3501 (adult female), from about 4.5 km (airline) NE of Monte Seco, 2630 m, 2 June 1987; USNM 292588 (adult female) and ANSP 31574–75 (adult female and male respectively), from 4 km (airline) NE of Monte Seco, 2550–2650 m, 23–24 January 1989; FMNH 232512 (adult male collected 7 May 1987), 231763 (subadult collected 24 June 1987), 231770 (adult male collected 24 June 1987), MHNSM 3502 (adult male), 3503 (subadult male), 3504 (adult female), collected 6 May 1987, and USNM 292587 (adult male), collected 28 January 1989, all from basecamp on trail between Monte Seco and Chorro Blanco, about 2.5 km (airline) NE of Monte Seco, 1800 m.

Definition.—The following diagnostic features (Lynch & Duellman 1973, Flores 1985) distinguish *C. euhystrix* from other *Centrolenella* species: (1) vomerine teeth absent; (2) bones green; (3) parietal peritoneum white, visceral peritoneum clear; (4) color in life: when active at night, dark greenish black with lighter green spicules; when concealed during day, nearly black; when active during day, dark green (brownish in sunlight) with light green spicules; color in preservative: dark gray to medium gray with white spicules; (5) finger webbing (I–II(2⁻)–(3.5)III(2.5)–(2⁺)IV); (6) toe webbing I(1)–(2⁻)II(1⁻)–(2⁺–2.5)III(1⁻)–(2.5)IV(3⁻)–(1)V; (7) head round in dorsal outline; snout truncate from above and truncate (slightly rounded in some females) in profile; (8) dorsal skin texture finely spinose with large pointed spicules in males, smoother in females; (9) ulnar and tarsal ridges absent; (10) no humeral spine; (11) tympanum two-thirds to completely visible; (12) prepollex

well developed, no externally visible prepollex spine; (13) nuptial excrescences white, forming large Type I pad; (14) no lateral glands; one pair of tubercles ventral to cloacal opening.

Description.—Head distinct, wider than body, wider than long, round in outline (most easily seen from below). Snout protruding, forming anterior outline of head viewed from above, truncate (occasionally with weak point) from above and truncate to slightly rounded (females) in profile, SL about 23% of HL; canthus rostralis straight, distinct, rounded in section; loreal region shallowly concave; lips not or only slightly flared. Nostril small, slit-like to elliptical, directed laterally on protuberance; internarial area flat to slightly concave. Eye moderate, directed slightly anterior of anterolaterally (>135°). Tympanum distinct, heavily pigmented, two-thirds to completely visible, dorsomedially inclined, posterolaterally directed; usually smooth or with low spicule; annulus tympanicus indicated as elevated and unpigmented border along anteroventral third to lower two-thirds of tympanum. Supratympanic fold heavy, especially in males, sometimes covering up to one-third of tympanum. Tongue round to weakly cordate. Vomerine teeth absent. Choanae round to slightly elongate, occasionally slightly rectangular, about size of subarticular tubercle on finger III, separated by distance 5.5 times their diameter. Vocal slits paired, elongate, posterolateral to tongue.

Dorsal skin texture of males finely spinose with large, white (in preservative), pointed (often more rounded medially) spicules; spicules sparsely distributed on snout and dorsum of head and best developed dorsolaterally, above tympanum, and on upper arms (Fig. 3); dorsal surfaces of limbs spiculate; spicules present on sides of head and legs, extending onto lateral sides of foot to basal part of digit V; lateral parts of body and dorsal surface of hands smooth. Dorsal skin of females much smoother,



Fig. 3. Adult male *Centrolenella euhystrix* (SVL 31.3 mm, FMNH 232513), collected on 2 June 1987 from about 4.5 km (airline) NE of Monte Seco, 2630 m, Department of Cajamarca, Peru.

spicules absent (usually) or sparsely distributed on sides of head, dorsolateral surface of body, and on limbs. Skin on belly variable (possible preservation artifact), nearly smooth or weakly to coarsely granulate, sometimes areolate; pectoral area and throat smooth; ventral surfaces of thighs weakly granulate. Moderately to poorly developed pair of cloacal (ventral to pubis) tubercles. Cloacal opening high between thighs; covered by moderately large flap with straight or slightly incised edge; flap margin smooth to crenulate; cluster of 0–9 spicules on each side below the opening.

Hands large (HnL/HL, 1.22); digits very wide, lateral ridges along all fingers. Digit lengths of hand I < II < IV < III; webbing absent between I and II, basal between II and III, moderate between III and IV; webbing formula I–II(2⁻)–(3.5)III(2.5)–(2⁺)IV. Thumb tip expanded, disc I 60% width of

discs III or IV; discs on fingers II–IV expanded, broader than disc I, those of III and IV about equal in width. Prepollical area enlarged, no external prepollical spine. Nuptial excrescences large, whitish, Type I. Subarticular tubercles present, that on finger IV largest. Inner metacarpal tubercle elongate; outer tubercle more elliptical, equal to or slightly smaller than inner. Small palmar tubercles at base of fingers. No fringes or tubercles along outer edge of forearm. Forearm larger than upper arm; no obvious sexual dimorphism. No humeral spine.

Digit lengths on foot I < II < III <=> V < IV. Webbing extensive, toe webbing formula I(1)–(2⁻)II(1⁻)–(2⁺–2.5)III(1⁻)–(2.5)IV(3⁻)–(1)V. All toe discs expanded; tip on toe I 60% of that on toe IV; discs on toes III–V about equal in size. No tarsal fold. Subarticular tubercles moderate, rounded, about of equal size. Distinct inner metatar-

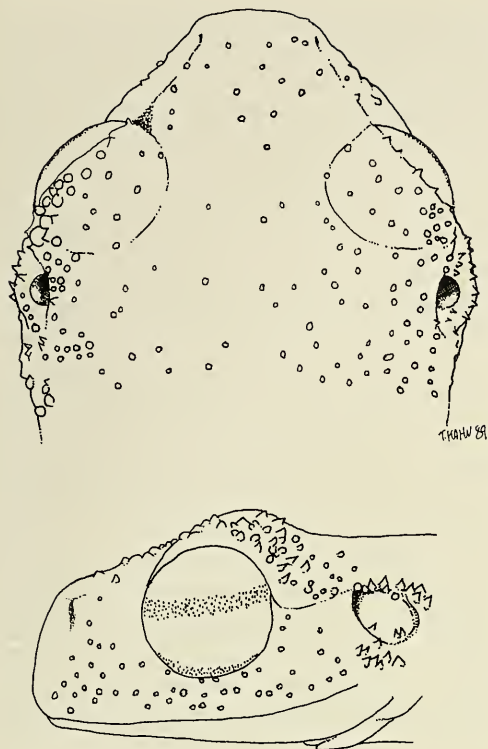


Fig. 4. Dorsal and lateral views of the head of the holotype of *Centrolenella euhystrix* (male, SVL 31.1, FMNH 232510).

sal tubercle, width about equal to tip of digit I; outer tubercle small, poorly developed.

Snout-vent lengths of adult males 28.5–31.3 mm; of adult females 31.1–33.6 mm.

Coloration.—In life the dorsum is dark greenish black in active individuals, and dark green in inactive ones. The head (especially eyelids and lips), back, and limbs of males are densely covered with large, light green spicules, lighter than dorsal ground color and giving a finely spotted appearance to dorsum. Females generally have smooth skin with few spicules on forelimbs, upper lip, and shank, and generally lack the spotted appearance. The venter is greenish with yellow wash on anterior belly region. The parietal peritoneum is white over anterior half of belly. The feet and hands are clear or greenish yellow with dull yellowish wash;

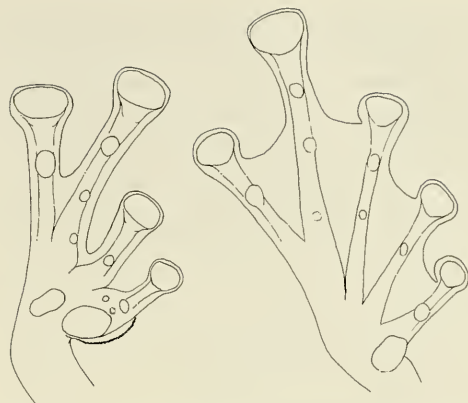


Fig. 5. Diagrammatic representations of the right hand and foot of the holotype of *Centrolenella euhystrix* (male, SVL 31.1, FMNH 232510).

the webbing is transparent yellowish. The bones are green. The irises of female (MHNSM 3504) and subadult male (MHNSN 3503) were “gray with fine black irregular reticulations” (Cadle, field notes); that of adult male (FMNH 232512) deep medium brown. In bright sunlight the dorsum changes to light greenish gray.

Centrolenella euhystrix is capable of rapid color changes from a uniform black to dull dark green. When collected, the holotype was totally black dorsally, with some yellow on the palmar and plantar surfaces, matching the black log under which it was found. After a short time in the collecting bag, this frog turned a dull dark green.

In preservative, dorsal surfaces of head, body, and limbs of males dark gray to medium gray, tubercles white; dorsal surfaces of hands, feet, and webbing pale gray; flanks gray, gradually lightening ventrally; venter creamish gray, palest on proximal parts of thighs and pectoral region; some males dark gray on chest and throat; nuptial excrescences creamish. Females pale to dark gray dorsally; creamish to gray ventrally. Nictitating membrane covered with gray melanophores except in central portion of upper half, which lacks pigment.

Measurements of holotype.—SVL—31.1;

HL—9.7; HW—11.0; ED—3.1; EN—2.2; SL—4.7; TW—0.65; TL—15.9; HnL—11.8.

Osteology.—A cleared and stained male specimen of *C. euhystrix* (SVL 31.0; FMNH 232511) has the prepollex completely enclosed within thumb base; the prepollex extends about 80% the length of metacarpal I. The tip of the prepollex is distinct, cartilaginous, with some mineralization (see Discussion for use of this term). Metacarpal III bears a medially projecting bony flange near the midpoint. Digit tips are T- to slightly Y-shaped; the intercalary elements are mineralized. The proximal flange (deltoid crest) of the humerus is about 45% the length of the bone; it lacks a projecting spine. The vomers are widely separated medially, embedded in the large cartilaginous floor of the nasal capsule, and lack teeth. The frontoparietal fontanelle is large; the anterior projections of the frontoparietals on the skull table overlap the sphenethmoid. The parasphenoid does not reach the level of the palatines. On the lateral surface of the braincase, the sphenethmoid is separated by a small cartilaginous gap from the posterior portions of the cranium. Quadratojugals are present but do not articulate with the maxilla. A cartilaginous annulus tympanicus and bony columella are present.

The hyoid of *Centrolenella euhystrix* differs from that illustrated by Eaton (1958, fig. 5) for *C. prosoblepon*. Eaton indicated only the bony posteromedial processes of the hyoid plate (Duellman & Trueb 1986, fig. 13.21), whereas the hyoid of *C. euhystrix* bears cartilaginous anterolateral and posterolateral processes as well. David C. Cannatella (pers. comm.) informed us that these processes are typical of *Centrolenella* hyoids and that Eaton's figure is erroneous in these details. In general form the hyoid of *C. euhystrix* is similar to that illustrated for *Lepidodactylus ocellatus* by Duellman & Trueb (1986, fig. 13.21D). The hyoid plate is broad, about 1.5 times as wide as long. The tips of the anterolateral processes are flared distally. The posterolateral processes are slightly

longer than the anterolateral processes, and tapered distally. The only bony elements of the hyoid are the posteromedial processes.

All digits have intercalary elements between the penultimate and ultimate phalanges, and in all cases these elements are mineralized (i.e., they stain red with alizarin; see Discussion for further consideration of terminology). In the hand the intercalary elements are as wide as the distal ends of the penultimate phalanges. They are proximo-distally compressed with the proximal surface slightly convex and the distal surface concave. The intercalary elements in the feet are of the same general form as on the forelimb. The epiphyses of all phalanges are well-mineralized.

Natural history notes.—At night, individuals of *Centrolenella euhystrix* were active mostly on vertical rockfaces in the splash/spray zone of waterfalls, on rock ledges (upper or lower surfaces) in or around waterfalls, and on liverwort- and moss-covered wet boulders in midstream. Most were located by eye-shine. Many individuals were observed on rock ledges in waterfalls 6–8 m high, but were too high to collect. At night their dark greenish bodies were difficult to see against the mosses and liverworts that usually cover their perches. A juvenile male (MHNSM 3503; 28.3 SVL) clung to a twig hanging from a vertical rock face 0.8 m above the water in a waterfall spray zone. Another individual was perched on a leaf over water at night. The holotype, the only individual found by day, was under a log in a pile of debris in the middle of a stream. In general, *C. euhystrix* seems to prefer microhabitats along streams close to water splashing or pouring over rocks.

Observations of the behavior of adult *C. euhystrix* are similar to those reported for *Centrolene geckoideum* in Colombia (Lynch et al. 1983). These authors reported female and calling male *Centrolene* on vertical or overhanging rock faces in the spray zones of waterfalls, and egg masses attached to the same rock faces. Given that virtually all in-

dividuals of *C. euhystrix* were associated with rock faces near or in waterfalls and that no egg masses attributable to this species were found attached to vegetation, we consider it possible that eggs of this species are attached to rocks as in *Centrolene*. Such behavior has not been reported for any species of *Centrolenella*.

Vocalization and reproductive behavior.—Males called from rock ledges or vertical faces at two sites around waterfalls at about 2600 m on 2 June. A lone male called from a large boulder 20 cm above a stream at 1800 m on 6 May. The call sites often were within the splash zone of small waterfalls and on dripping rock faces covered with mosses and liverworts. The call is a short “click” or “chirp” usually given as two notes in rapid succession; occasionally a call consisted of only a single note. Although no individuals were heard calling in January 1989, the noise from the torrential streams which are excessively swollen during the rainy season, may have precluded hearing the calls. One female (MHNSM 3504) was collected 0.3 m above the rushing stream and was difficult to see on the bryophyte-covered rock. Two frogs were found in close proximity on a vertical rock face in a spray zone of a waterfall on 23 January. The male (ANSP 31575) was above the female (ANSP 31574) but mostly lateral to her body, and the pair was not observed in amplexus. Possibly, the pair had been disturbed by the observer before they were noticed. The male rapidly ascended the rockface when a light was shone on them. No egg masses that we could attribute to this species were found.

Distribution.—*Centrolenella euhystrix* is known only from two streams at the type locality and from about 2.5 km (airline) NE of Monte Seco at 1800 m along a trail to Chorro Blanco (Fig. 2). Monte Seco is a coffee cooperative located approximately 80 km ESE of Chiclayo. The type locality is along an abandoned logging road that parallels the ridge to the northeast of Monte Seco. Chorro Blanco is a waterfall near the

site of Cadle’s field camp. The recorded elevational range is 1800 m to 2630 m.

Etymology.—The specific epithet “euhystrix” is derived from the Greek word “hystrix,” meaning porcupine, and the prefix “eu,” meaning very. We use it as a noun in apposition to refer to the very spiny, porcupine-like dorsum of males of *euhystrix*, which for a centrolenid is quite unusual.

Centrolenella hesperia, new species

Figs. 6–8

Holotype.—Field Museum of Natural History (FMNH) 236200 (field number J.E. Cadle 9260), an adult male, taken near the basecamp on trail between Monte Seco and Chorro Blanco, about 2.5 km (airline) NE of Monte Seco, Río Zaña, Department of Cajamarca, Peru, 1800 m (Fig. 2). Collected 28 Jan 1989 by J. E. Cadle.

Paratypes.—Sixty-seven specimens with the following data: FMNH 232495, 232503 (adult females), 232496–232501, 232504–232508 (adult males), 232502 (adult male, cleared and stained), and MHNSM 3505–3507 (adult males), 3508–3509 (adult females), collected between 6 and 17 May 1987; USNM 292582, 292584 (adult males), 292583 (adult female), and ANSP 31576, 31586, 31588 (adult females), 31577–85, 31587 (adult males) collected 14 Jan 1989; USNM 292585 (adult male) and ANSP 31601–06, 31608 (adult males), 31607 (adult female) collected 18 Jan 1989; USNM 292586 (adult male) and ANSP 31609–13, 31615–18 (adult males) and 31614 (adult female) collected 28 Jan 1989; all from same locality as holotype. ANSP 31589–90, 31592–94 (adult males), 31591 (adult female) from 1.5 km (airline) NE of Monte Seco on trail to Chorro Blanco, 1530 m, and ANSP 31595–98 (adult males), 31599–600 (adult females), from the same locality at 1630 m, 15 Jan 1989.

Definition.—The following diagnostic features (Lynch & Duellman 1973, Flores 1985) distinguish *C. hesperia* from other



Fig. 6. Adult male *Centrolenella hesperia* (SVL 26.0, FMNH 232501), collected on 8 May 1987 from 2.5 km (airline) NE of Monte Seco, 1800 m, Department of Cajamarca, Peru.

Centrolenella species: (1) vomerine teeth absent; (2) bones green; (3) parietal peritoneum white, visceral peritoneum clear; (4) color in life leaf green with green spicules, light lateral stripe, and white cloacal patch; in preservative pale lavender with irregularly placed, pigmentless spots surrounding large, white spicules, giving the appearance of light-colored dots; (5) webbing formula on fingers I-II(2⁺)-(>3.5)III(3⁻)-(2.5)IV; (6) webbing on toes I(2⁻)-(2.5)II(1⁺)-(2⁻-2.5)III(1⁺-1.5)-(3⁻-3.5)IV(3⁺)-(1.5-2⁻)V; (7) head round in dorsal outline; snout weakly truncate from above, obtuse to moderately sloped in profile; (8) dorsal skin texture in males shagreen with minute spicules and scattered larger spicules, smoother in females; (9) ulnar and tarsal ridges present; (10) humeral spine present in males; (11) tympanum not visible; (12) prepollex slightly enlarged, lacking an external prepollical

spine; (13) creamish nuptial excrescences, Type I pad; (14) no lateral glands; one pair of tubercles ventral to cloacal opening; skin beneath cloacal opening thickened, appearing glandular.

Description.—Head wide, 1.2 times length, only slightly wider than body, round in outline. Snout short (SL about 18% of HL), not or only slightly protruding, weakly truncate in dorsal outline, obtuse to moderately sloped in profile; canthus rostralis indistinct; loreal region weakly concave to flat, slightly obtuse; lips slightly flared. Nostrils oval to slitlike, slightly recessed, directed posterolaterally; internarial area concave to nearly flat. Eyes small, directed slightly anterior of 135°. Tympanum not differentiated externally; annulus tympanicus not obvious, tympanic region usually indicated by raised area which, when present, is most distinct anteroventrally. Supratym-



Fig. 7. Dorsal and lateral views of the head of the holotype of *Centrolenella hesperia* (male, SVL 25.5, FMNH 236200).

panic fold indistinct. Tongue round to oval, slightly broader anteriorly, occasionally slightly notched anteriorly and posteriorly. Vocal slits large, posterolaterally situated. No vomerine teeth. Choanae round, about 30–40% width of pad on finger I; separated by distance about four times their diameter.

Dorsally, skin in males shagreen with minute spicules and larger, scattered spicules with white tips; spicules smaller and densest on lip below eye and below tympanic area on head, larger and more evenly distributed on back, somewhat sparser on snout and upper surfaces of limbs; skin smooth or with few scattered spicules in fe-

males; lateral (below stripe) skin smoother, without spicules; ventral skin coarsely and uniformly granulate on belly, smooth on throat and chest, less granulate on ventral surfaces of thighs. Moderately developed pair of ventral tubercles below cloacal opening. Cloacal opening on upper quarter between limbs, subterminal (visible from above), covered by straight-edged (rarely weakly scalloped), shallow flap; area below cloacal area appears glandular.

Hands moderately large (HnL/HL, 1.19); order of finger lengths $I < II < IV < III$. Finger webbing absent between digits I and II, basal between fingers II and III, and slight between III and IV; formula $I-II(2^+)-(>3.5)III(3^-)-(2.5)IV$. Ridges along lateral edge of all digits, especially well developed on lateral margins of II and III, and on medial margin of IV. Tip of thumb slightly expanded, about 55% of disc III; disc III widest, discs II and IV about equal. Pre-pollical area moderately expanded, no external prepollical spine. Nuptial excrescences cream-colored but not greatly enlarged, Type I pad, relatively large cells on ventral surface of thumb base. Subarticular tubercles low, round, largest on finger IV. Metacarpal tubercles indistinct, inner elongate to kidney-shaped, outer more oval; palm tubercular. Ulnar fringe distinct, extending onto hand. Humeral spine present, not protruding externally. Forearm larger than upper arm, no obvious sexual dimorphism in arm size.

Toe lengths $I < II < III < V < IV$. Toe webbing smooth to granulate, of moderate extent; webbing formula $I(2^-)-(2.5)II(1^+)-(2^-2.5)III(1^+-1.5)-(3^-3.5)IV(3^+)-(1.5-2)V$. Thumb disc slightly expanded, 60% of width of disc IV; disc IV widest, III and V about equal. Lateral tarsal ridge extending onto base of digit V. Subarticular tubercles moderate, rounded. Inner metatarsal tubercle small, elongate, slightly larger than low outer tubercle, both weakly developed.

Snout–vent lengths of adult males 23.0–27.3 mm; of adult females 24.7–28.8 mm.

Coloration.—In life, the dorsum of *C. hesperia* is light leaf green with pale green spicules on upper surfaces of limbs, head, and body (Fig. 6). A pale cream upper labial stripe continues laterally along the body to the groin, and separates the dorsal color from the yellowish cream ventral color. The irises are grayish white with black reticulations. Ventral surfaces of throat and shank are clear green. Feet, webbing, and ventral surfaces of thighs have a yellow wash. Anterior belly region is cream to yellowish cream. Parietal peritoneum is white over most of belly. A white rump patch is present. A white line runs along the outer border (with frog in sitting position) of the limbs. The bones are green.

In preservative males are pale lavender with some scattered, irregular pigmentless spots and white spines giving the appearance of pale dots; females are uniform lavender with a few irregular pale areas. The upper lip is pale, without pigment. Eyelids also lack pigment except for a few melanophores along the upper margins and more at the bases. Under $20\times$ magnification melanophores on some specimens are arranged in a circular pattern in the ear region. A sharply demarcated line occurs laterally between the dorsal pigmentation and the light unpigmented sides. Venter is creamy white; palmar and plantar surfaces and webbing are white. White labial, lateral, ulnar, and tarsal lines, and a white rump patch are visible in specimens preserved less than eight months but not visible in the 1987 sample. (This may reflect some difference in preservation between samples rather than fading.)

Measurements of holotype.—SVL—25.5; HL—7.8; HW—9.2; ED—2.6; EN—1.4; SL—3.4; TL—14.5; HnL—9.3

Osteology.—A cleared and stained male specimen (22.2 SVL; FMNH 232502) has a prepollex that extends about 75% of length of metacarpal I and is completely enclosed within the thumb base; a non-mineralized cartilaginous tip is distinct. Metacarpal III

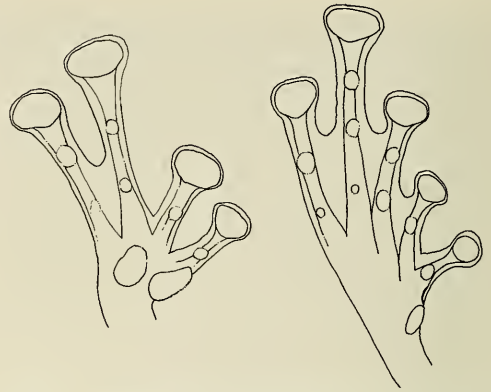


Fig. 8. Diagrammatic representations of the right hand and foot of the holotype of *Centrolenella hesperia* (male, SVL 25.5, FMNH 236200).

has a medial bony flange with cartilaginous anterior and posterior borders. The tips of the digits are T- or shallowly Y-shaped; intercalary elements are mineralized. The proximal flange (deltoid crest) of the humerus bears a distal projecting spine that extends about half the length of the flange. The vomers lack teeth and are embedded in the cartilaginous matrix of the floor of the nasal capsule. The frontoparietal fontanelle is large; anterior projections of the frontoparietals on the skull table narrowly overlap the sphenethmoid. The anterior tip of the parasphenoid nearly reaches the level of the palatines. On the lateral surface of the braincase, the sphenethmoid is separated by a large cartilaginous gap from the posterior cranial elements. The quadratojugals are present but do not articulate with the maxilla. A cartilaginous annulus tympanicus and bony columella are present.

The hyoid structure of *Centrolenella hesperia* is similar to that described previously for *C. euhystrix* with two exceptions. The distal tips of the anterolateral processes are irregularly-shaped and not expanded as in *C. euhystrix*. In *C. hesperia* the posterolateral process on the right side is interrupted by a small non-cartilaginous gap and is less robust than on the left side, which bears a complete process. Undoubtedly, this is an

individual aberration or artifact of preparation, but it may reflect a developmental source of variation in this structure for this or other species of *Centrolenella*.

Intercalary elements are present between the penultimate and ultimate phalanges of all digits. These elements are small (narrower than the distal end of the penultimate phalanx) and of the same form but not as well mineralized as those in *C. euhystrix*. In the hand only a trace of mineralization is evident in the intercalary element of digit I. The intercalary elements in the foot show a progressive increase in mineralization from that in digit I, in which no mineralization is detectable, to that in digits IV and V, which are well mineralized. A similar pattern of mineralization was observed in a preparation of *C. orientalis* (USNM 257182). The epiphyses of all phalanges are entirely cartilaginous.

Natural history notes.—At night nearly all individuals were perched on the upper surfaces of leaves over streams. One female (FMNH 232503) was found by day, apparently having been disturbed during survey work. She was hopping on the litter in low vegetation >30 m from the nearest stream. Several others were observed during the day as they rested vertically on upper leaf surfaces over streams where breeding occurred.

Breeding in this species apparently begins with the onset of rains. Males call from the upper surfaces of leaves 0.5–3 m above streams. In 1989, regular daily rains did not begin until 20 January (as inferred from degree of soil moisture and interviews with locals), and this coincided with males calling regularly each night. A search for eggs along two streams on 14 January revealed only a single mass, despite many calling individuals on that date. Within two weeks, however, egg masses along these streams were abundant. During the dry season males were calling between 6 May and 15 June, but none thereafter (Cadle left the field site on 25 June).

Although no males were individually

marked, it is our impression that males are active at the same site for several nights and may attract more than one female. Multiple egg masses in different developmental stages often were seen on the same or adjacent leaves near a calling male. As many as four masses, three with eggs in different developmental stages ranging from early neurula to near-hatching, and the jelly remains of another clutch already hatched, were observed in the same bush near one male on 7 May. Males (presumably the same individuals) were observed calling from the same sites over the span of several days. Male densities often were very high, as was breeding activity (based on the number of observed egg masses in some stream sections) compared to our experience with other species of the genus. In two frequently-worked sections of stream, male densities sometimes exceeded 30 individuals along approximately 10 m. Densities apparently depend primarily on the amount of foliage available for perches.

Although only one kind of vocalization was noted, aggressive interactions occurred among males. On 7 May at 2204 hr, two males (MHNSM 3505, 23.0 mm SVL; 3506, 24.3 mm SVL) were observed fighting belly-to-belly on the petiole of an elephant-ear leaf (Araceae) in a head-to-vent position. They released their grappling holds when disturbed by the light. Grappling or similar behavior between males has been observed in other species of *Centrolenella*: *C. fleischmanni* in Mexico and *C. valerioi* in Costa Rica (McDiarmid & Adler 1974), *C. griffithsi* in Ecuador (Duellman & Savitzky 1976), *C. fleischmanni* and *C. prosoblepon* in Costa Rica (Jacobson 1985), *C. prosoblepon* in Panama (Jungfer 1988), and in Ecuador (McDiarmid, unpublished field notes), and is not unexpected in high-density situations especially among territorial males. This head-to-vent position has not been observed previously, but we are not surprised and view it as another variant of the several grappling positions reported. Males of many

centrolenid species equipped with specialized morphological structures (e.g., humeral hooks or spines, prepollical spines) are territorial (McDiarmid, unpublished notes) and use them in an aggressive fashion against other males during fights over calling and egg-laying sites. The outcome of the fight, not the positions assumed by the combatants during the grappling, is the more significant parameter. Taylor's suggestion (1949) that the prepollical spines in *Centrolenella spinosa* serve as a grasping organ during mating has not been supported by field observations and seems highly unlikely to us. Likewise, suggestions in the literature that the humeral spines in *Centrolene geckoideum* may have some scansorial function, perhaps enabling an individual to maintain its hold on a tree (Noble 1920), or in other species (e.g., *Centrolenella prosoblepon*) apparently functioning to insure amplexus (Noble 1924) or involved mechanically in amplexus (Eaton 1958) also are unverified and lack merit. We have seen mating pairs of several species (including *C. prosoblepon*) whose males have humeral spines, and in no instance did the males insure their grips on the females or otherwise use their spines during amplexus. We contend that humeral spines are secondary sexual traits used by males to defend their territories from other males and in this sense are analogous to horns in certain territorial mammals.

Centrolenella hesperia lays light greenish-white eggs in a single, loosely arranged layer on the upper surfaces of leaves above water, usually on the distal quarter of the leaf near its tip. Egg masses (FMNH 232713–15; ANSP 31619–21; USNM 292591) were found on ferns (*Polystichum*), a melastome, leaflets of a small palm, elephant ears (Araceae), and other understory plants along the stream margins. In two or three instances masses were attached to aerial roots of epiphytes situated on tree limbs overhanging the water.

An egg mass (FMNH 232715) taken from a leaf 1.5 m above the water at 2114 hr on

7 May contained 26 light green eggs in Gosner stage 1. These eggs measured about 2.2 mm diameter and may have been laid earlier that evening. A calling male (FMNH 232508, SVL 25.7) was collected on the same bush about 1.0 m above the water. Another egg mass (USNM 292591) collected during the day of 29 January contained 38 eggs in stages 4 and 5 that measured 2.5 to 2.7 mm diameter. A sleeping male was found on top of a leaf near this clutch. This clutch of 38 eggs was attached to the upper surface of a fern frond (*Polystichum* sp.) and had 16 empty capsules on its proximal (top) edge (Fig. 9). All egg masses examined had empty capsules on the side closest to the leaf petiole. Empty capsules have been observed in egg masses of certain other *Centrolenella* species (McDiarmid, unpublished field observations) but not with the apparent consistency of this species. Because the capsules are always positioned along the upper edge of the clutches of *Centrolenella hesperia*, we suspect that they may function to increase the adhesion of the egg mass to the leaf or, by way of their hygroscopic tendencies, retain water and serve as an additional water source for the eggs during their several days of development when they are exposed to the air.

The size of 12 "dry season" clutches (2–9 May) range from 16 to 30, $\bar{X} = 20.7 \pm 4.4$. This is significantly smaller than the size of 15 clutches laid at the beginning of the "wet season" (29 Jan), range 19–42, $\bar{X} = 33 \pm 6.9$ (*t*-test for difference between the means, *t* = 4.096, *P* < 0.001).

Some observations suggest that loss of egg masses due to desiccation was a problem in 1987 for those laid after mid-May. Breeding activity for this species, as indicated by the number and regularity of calling males and recent egg masses, declined rapidly after mid-May. By this time the regular rains had ceased, fogs characteristic of the site were less intense and enduring, and the humidity was lower. The last viable clutches were observed on 25 May, when three masses with

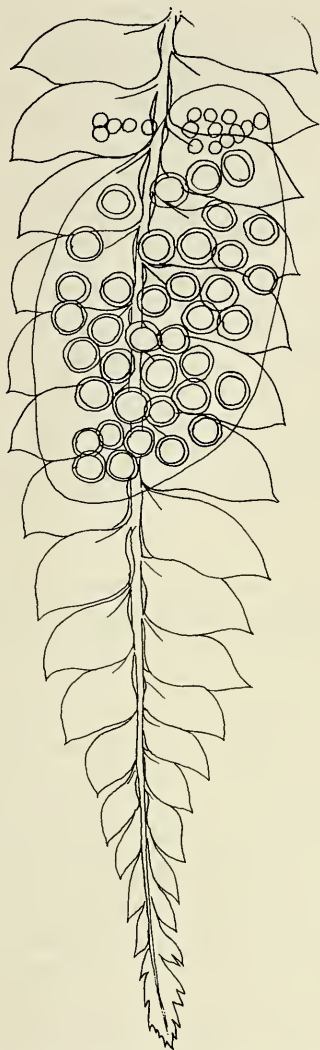


Fig. 9. Drawing of an egg mass (USNM 292591) of *Centrolenella hesperia* attached to the upper surface of a fern (*Polystichum* sp.) frond showing the position of the 38 eggs and 16 capsules. Line equals 20 mm.

advanced tadpoles were found along the stream where most of the previous breeding activity had occurred. Two desiccated clutches and no fresh egg masses were observed here on 15 June. On 26 May along another stream two desiccated clutches were found on the same palm frond where viable clutches had been seen earlier in the month.

At 2055 hr on 7 May, a male was calling about 40 cm from a female that was alone

on top of an egg mass. When checked at 2248 hr the male was still calling but the female was gone; 17 eggs were in the clutch. At the time Cadle pondered the meaning of this behavior and wondered whether the female was performing some egg-laying activity in the absence of the male. More detailed observations of what appears to be the same behavior were made later at a different site on the same stream. On 10 May a female (FMNH 232495; 28.8 SVL) was found at 2116 hr next to an egg mass. When first observed, the female was flattened against the leaf in a normal sitting position with her cloacal opening oriented above the upper (proximal for the leaf) edge of the mass containing 16 recently laid eggs. After maintaining this position for several minutes, she raised the rear part of her body, and at the same time positioned her thighs perpendicular to the body axis. She held this new position for several minutes. During the next hour, the female alternated several times between this behavior and the more normal sitting position, at which time the frog was collected.

We do not understand the significance of these females' behavior. We do not think that the females were depositing eggs independently of the males, and no issuances from the cloaca were observed. Dissection of female FMNH 232495 revealed small ova in the right ovary, and small, as well as somewhat larger ova in the left ovary. No eggs were present in the body cavity or oviducts (which were enlarged). These observations suggest that she was not ready to lay eggs when collected, but the enlarged oviducts indicate that she may have recently laid eggs. We speculate that the females were: (1) wetting the egg mass (likely their own and presumably with water stored in their bladder), a behavior that has been reported for males of *C. fleischmanni* in Costa Rica (Jacobson 1985, Mark Hayes, pers. comm.); (2) depositing empty capsules in the mass presumably just after depositing the eggs (see previous discussion); or (3)

pressing the eggs against the leaf surface to increase adhesion. Aichinger (1987) reported a similar behavior by female *Hyla brevifrons* that he described as brushing the eggs into a monolayer. Because rain is more likely to detach an egg mass placed on the upper surface of a leaf than one placed on the lower surface of a leaf, and because the choice of an egg deposition site apparently is species-specific, those species that place their eggs on the upper surface of leaves might be expected to have behaviors that increase egg mass adhesion. We suspect (but did not observe) that the females' behavior was associated with depositing empty egg capsules, but cannot rule out the other two explanations. Whatever the functional significance of this peculiar behavior in females might be, to our knowledge it has not been reported previously in species of *Centrolenella*.

Larvae.—A few tadpoles (FMNH 232710–232712) were reared to stage 25 (Gosner 1960) from clutches taken from leaves in the field. The largest of these measured 14.9 mm total length with a tail 10.2 mm long. The tadpole is typical of centrolenids and has a fusiform body, rounded snout, and long, narrow tail. The eyes are small, crescent-shaped and dorsally located. The nostrils are located slightly closer to the eye than to the tip of the snout. Near the midpoint of the tail, the ventral fin is slightly deeper than the dorsal fin, and each is about 20% of the tail height. The tail has a rounded tip. The spiracle is small, oval, and opens posterolaterally about three-fourths of the way back on the left side of the body below the midline. The vent tube is medial. The oral disc is anteroventral and has a uniserial row of about 22 large marginal papillae laterally and posteriorly (the anterior edge is bare). Jaw sheaths are narrow, weakly keratinized, and serrate; they appear striated. The labial tooth rows are barely visible and not completely keratinized; A-2 has a wide medial gap; the short sections are located nearly lateral to the anterior jaw sheath. The labial tooth row formula is 2(2)/3.

Vocalizations.—*Centrolenella hesperia* has a short, two-note, high-frequency call (Fig. 10). A calling male (FMNH 232499, SVL 25.4) was recorded on 8 May 1987. The only air temperature data available are maximum (26°C) and minimum (10°C) values recorded for that day. An analysis of seven calls shows the following call characteristics (means are given with ranges in parentheses). The call consists of two notes with an overall duration of 0.12 sec (0.10–0.13). The first note has either two distinct pulses (two calls) or three distinct pulses (five calls) with an overall duration of 0.04 sec (0.03–0.05). The second note, consisting of one (occasionally two) pulses, lasts 0.02 sec (0.02–0.03) and is separated from the first note by 0.05 sec (0.04–0.06). In both notes the dominant frequency of the call is in the 3300–4000 hz range (mean about 3630 hz). Calls (Fig. 10) were given at a rate of about two per second. The pulse rate calculated for the first note was 71.4 notes per second (62.5–76.9). The rise time for these pulses is very fast, averaging 0.0014 sec (0.0008–0.0025).

Distribution.—*Centrolenella hesperia* is known only from the vicinity of the type locality (Fig. 2). The recorded elevational range is 1500 m–1800 m. Although stream inaccessibility made searching extensively above 1800 m difficult, this species does not appear to occur above 2500 m where its detection would have been likely.

Etymology.—The specific epithet "hesperia" is a Latinized word derived from the Greek "hesperos" meaning western or of the evening. We use it as an adjective in reference to its being one of two species of *Centrolenella* first recorded from western Peru, and in reference to its evening activities.

Discussion

Comparisons.—We do not understand the relationships among centrolenid frogs. In part this is due to the incredible rate at which new species have been discovered and de-

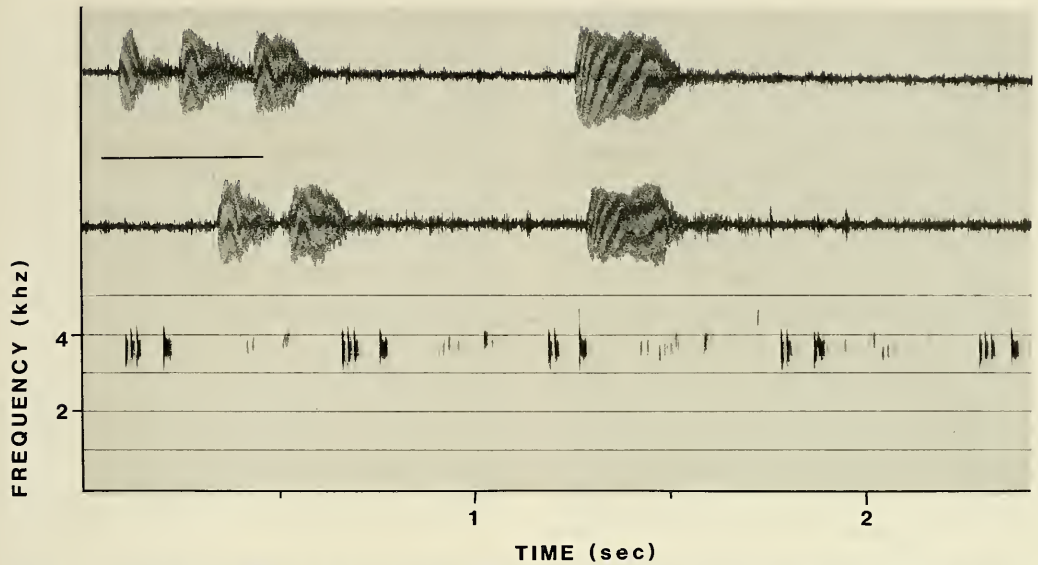


Fig. 10. Audiospectrograms of five advertisement calls of a male *Centrolenella hesperia* (SVL 25.4, FMNH 232499) with a wide-band filter (300 Hz). Calls were recorded on 8 May 1987 at the type locality. Waveforms of the first and third calls are shown above the audiospectrogram. Line between waveforms represents 0.034 sec.

scribed. By our calculation about 80% of the recognized species (Frost 1985 and publications since) in the family have been described in the past 30 years and nearly 30 species (>40% of the total described species diversity) in the past 10 years. The number of known but undescribed species also is quite high. In addition to the two we describe here, we know of three others from Peru, four from Ecuador, and four or more from Venezuela that are undescribed; Pedro Ruíz-Carranza (pers. comm.) informed one of us of a large number of undescribed forms from Colombia.

Moreover, the lack of detailed comparative morphological descriptions has precluded a comprehensive phylogenetic treatment of the family. Consequently, the presently recognized genera and species groups do not easily accommodate many of the species being described. This problem stems at least partly from the relatively recent recognition of the family (Taylor 1951) and partly because two of the genera proposed in that paper were inadequately defined and generally have not been accepted

(Goin 1964, Savage 1967). When species groups have been proposed (Savage 1967, Savage & Starrett 1967, Starrett & Savage 1973), coverage has been restricted to geographic regions (i.e., Costa Rica or lower Central America), and the groups were subsequently claimed not to accommodate easily some species from other geographic regions (Lynch & Duellman 1973). These latter authors recognized the problems associated with species-group definitions based on geographic subsets (they reported species from Ecuador) of the family and preferred not to alter previous groupings or propose new ones.

We do not attempt to evaluate critically the various groupings that have been proposed within the family. We also recognize that our groups are ones of convenience and may not be monophyletic lineages, but for purposes of comparison we use the following five groups of centrolenids. (1) The genus *Centrolene* Jiménez de la Espada (see Ruíz-Carranza et al. 1986 for diagnostic traits), which includes two described forms (large species, presumably with exposed hu-

meral spines in males) and probably some undescribed ones. (2) Species within the currently recognized genus *Centrolenella* Noble (type *C. antioquiensis* Noble) made up of smaller species, the males of which have humeral spines (part of Savage's [1967] *prosolepon* group). (3) A second group within *Centrolenella* that includes species in which males lack humeral spines. This cluster of species also is part of Savage's *prosolepon* group; and if shown to be taxonomically distinct, they would be placed in Taylor's (1951) genus *Cochranella* (type *C. granulosa* Taylor). (4) Another group currently within the genus *Centrolenella* includes several small species with distinguishing characteristics (clear parietal peritoneum, no humeral spines, white color in preservative). This group, originally defined by Savage (1967) and Starrett & Savage (1973), has found general acceptance and has been referred to in the literature (Lynch & Duellman 1973, Cannatella 1980, Cannatella & Lamar 1986) as the *fleishmanni* group. As currently understood, this group has no available taxonomic name. (5) A final group currently placed within *Centrolenella* includes those species with prepollical spines. This trait was recognized by Taylor (1951) in his description of the genus *Teratohyla* (type *C. spinosa* Taylor). Two species (*C. gemmata* and *C. lynchi*) with prepollical spines also have humeral spines (Flores 1985) while the third, *C. spinosa*, does not. For this discussion, we include *C. gemmata* and *C. lynchi* in group 5.

Centrolenella euhystrix lacks humeral spines and therefore is associated with species in our group 3. The absence of humeral spines will distinguish it from all species of *Centrolene* (group 1) and those species of *Centrolenella* in group 2. *Centrolenella euhystrix* also lacks prepollical spines and thus differs from species in group 5. Though similar to members of the *fleischmanni* group (group 4 above) in that they all lack humeral spines and vomerine teeth, *C. euhystrix* is easily distinguished from all species in group

4 (characteristics in parentheses) by the following: larger size (usually less than 25 mm SVL), spinose skin (smoother skin), coloration in life dark green to nearly black without spots (pale green or yellow green with diffuse yellow spots or with pale reticulation) and in preservative dark gray (creamy white), truncate snout (truncate or rounded), distinct canthus (often flattened), and white parietal peritoneum (clear parietal peritoneum).

Centrolenella euhystrix lacks vomerine teeth and so differs from many species in group 3 which also lack humeral spines but have vomerine teeth. The following combination of characters distinguishes *C. euhystrix* from other group 3 species that lack vomerine teeth: green bones, large hands with wide digits and expanded toe tips, extensive toe webbing, color in life dark greenish black without light or dark flecks, spots, or ocelli, dark gray in preservative, and prominent (in males) pale green (life) or white (in preservative) spines on dorsum.

In comparison to the eleven currently recognized species of *Centrolenella* from Peru (Cannatella & Duellman 1982, Flores & McDiarmid 1989), *Centrolenella euhystrix* can be distinguished from all by its larger size, dark coloration in life and in preservative, and the extremely spinose dorsum of males. Other differences from Peruvian species include the following (characteristics of *euhystrix* in parentheses): *C. azulae*, *C. spiculata*, and *C. midas* have vomerine teeth (lacking); *C. bergeri* and *C. munozorum* have white bones and concealed tympana (green bones and visible tympanum); and *C. phenax* has a clear parietal peritoneum (white).

The only species on the western versant of northern South America that approaches *C. euhystrix* in size, webbing, and coloration is *C. orejuela* (Duellman & Burrowes 1989), but this species is reported to have vomerine teeth, smooth skin, and white visceral peritoneum. We note that the holotype of *C. orejuela*, reported as an adult female by Duellman & Burrowes (1989:5), in fact is

an adult male with vocal slits and large nuptial pads. Also, the paratype (IND-AN 1520) illustrated in Duellman & Burrowes' paper (1989, fig. 1) is listed as a female in the caption but as an adult male in the text.

In many respects (size, coloration, spinose dorsum, absence of vomerine teeth, webbing) *C. euhystrix* is similar to *C. johnelsi* (Cochran & Goin 1970) from northern Colombia. However, *C. johnelsi* has humeral spines and smaller finger discs. The closest relative of *C. euhystrix* may be found among several undescribed species recently collected from the Amazonian side of the Andes in northern Peru, or perhaps in other areas of northern Peru or southern Ecuador (see below).

Centrolenella hesperia (placed in our group 2) has humeral spines and thus is distinct from members of groups 3, 4, and *C. spinosa* in group 5. It also is distinct from *C. gemmata* and *C. lynchi*, two species with both humeral spines and prepollical spines (prepollical spines are lacking in *C. hesperia*). This species is easily distinguished from the described species of *Centrolene* (group 1) by the following traits: smaller size (<30 mm vs. >45 mm in *Centrolene*), concealed humeral spine (exposed in *C. geckoideum*), proportionally broader head (HW/SVL about 36% vs. <28% in *Centrolene*), concealed tympanum (visible), lack of vomerine teeth (present or absent), and light eggs (dark eggs).

Among species in group 2, *C. hesperia* differs from those with vomerine teeth by lacking vomerine teeth, and from many others by having a uniform green dorsum with small spines. It can be distinguished from *C. johnelsi* and *C. pipilata*, two species with spines, by its lavender color in preservative (gray or purplish gray) and concealed (distinct) tympanum. The combination of humeral spines, spiculate and spinose dorsum, concealed tympanum, and moderately sloped snout distinguishes *C. hesperia* from nearly all other species of *Centrolenella*. It is the only described species with a distinct

white lateral line, white cloacal patch, and ulnar and tarsal ridges.

Of the described Peruvian species of *Centrolenella*, *C. hesperia* can be distinguished from all as follows (characters of *C. hesperia* in parentheses): *C. bejaranoi*, *C. midas*, *C. ocellata*, *C. phenax*, *C. pluvialis*, *C. spiculata*, and *C. truebae* lack humeral spines in males, have visible tympana, and lack lateral stripes (present, absent, and present, respectively). In addition, *C. midas* and *C. spiculata* have vomerine teeth (absent). *Centrolenella bergeri* and *C. munozorum* have white bones and lack humeral spines and lateral stripes (green bones, spines and stripes present). *Centrolenella azulae* has a visible tympanum and vomerine teeth (tympanum and vomerine teeth absent). *Centrolenella mariae* has a visible tympanum and no lateral stripes (undifferentiated tympanum and lateral stripes). Males of *C. mariae* remain unreported so that the condition of the humeral spine is unknown.

As with *C. euhystrix* from this locality, the closest relative of *C. hesperia* may be found among several undescribed species from Peru's Amazonian slopes. However, some species at Monte Seco are distributed through the Huancabamba Depression area of northern Peru (Amazonian versant), in other areas of northwestern Peru or western Ecuador (Pacific versant), or have their closest relatives in these areas (Fig. 1). Examples include *Dendrophidion brunneum*, which has a narrow distribution along the Pacific versant of Ecuador and northern Peru (Lieb 1988); *Eleutherodactylus lymani*, widely distributed throughout the Huancabamba Depression and southern Ecuador (Lynch 1969); and *Coniophanes longinquus*, which is closely related to *Coniophanes dromiciformis* of southwestern Ecuador (Cadle 1989). *Centrolenella euhystrix*, *Centrolenella hesperia*, and their close relatives possibly have distributions similar to these, but resolution of this problem must await adequate delineation of species groups within the genus.

Intercalary elements and their descriptors.—Because the family Centrolenidae has been characterized by the presence of cartilaginous intercalary elements between the penultimate and ultimate phalanges (Duellman 1975, Duellman & Trueb 1986, Duellman 1988), our discovery that these elements are mineralized in the two species of *Centrolenella* described herein was, to us, somewhat surprising, although David C. Cannatella (pers. comm.) informed us that this condition is common in centrolenids. Certain descriptors (e.g., “ossified,” “mineralized,” and “calcified”) have been used indiscriminately in the literature to describe the nature of intercalary elements in some frogs. Such use can lead to misinterpretations and subsequent confusion. For example, in their description of *Scarthyla ostinodactyla* Duellman & de Sa (1988) used all three terms to describe the intercalary elements of hyloid frogs but did not distinguish clearly among their use. The confusion arises because several types of tissues, including cartilage, can receive deposits of calcium salts by a variety of processes. These tissues then become red with alizarin stain in the standard cleared and stained whole-mount preparations used for anuran osteological studies. Drewes (1984) noted that in most adult hyperoliids, the intercalary “cartilages” are partly or wholly mineralized (i.e., stain red with alizarin), and used the term “intercalary elements” and the descriptor “mineralized” to refer to these structures. We prefer this terminology for the following reasons. The terms “calcified” (as used with reference to cartilage) and “ossified” (used specifically with reference to bone) have precise meanings in the histological and anatomical literature that imply specific processes by which a tissue becomes impregnated with calcium deposits. Calcified cartilage and bone are distinguished, among other things, by differences in vascularity, growth properties, extracellular matrix components, and cell types involved (see Ham & Cormack 1979, Poole et al.

1989). Because these features rarely are studied in evaluating the nature of intercalary elements in anurans, and in any case cannot generally be distinguished in cleared and stained preparations, a need for precise usage of these terms exists. We argue that the term “mineralized” is most appropriate to describe those intercalary elements that have calcium deposits and for which the mechanism of deposition has not been determined histologically; this term does not imply the specific process or histological structure involved. Noble & Jaeckle (1928: 271) reported that the intercalary element in *Polypedates leucomystax* occurs as “. . . fully ossified bone with a marrow cavity. . . .” Drewes (1984) examined histological sections of the intercalary element of *Kassina senegalensis*, a species with a similarly appearing and identically shaped intercalary element to that of *P. leucomystax*, and found only calcified cartilage. This condition appears to be characteristic of nearly all mineralized intercalary elements that have been studied histologically in anurans (David C. Cannatella, pers. comm.). We suggest that “mineralized” be used as a descriptor when only a gross characterization is available (as in cleared and stained preparations).

Our reading of the literature suggests that most workers use the terms “intercalary cartilages” or “cartilaginous intercalary elements” to refer to non-mineralized intercalary cartilages, whereas both “ossified” and “calcified” have commonly referred to intercalary elements composed of calcified cartilage (for which we prefer the term “mineralized”). According to Duellman & de Sa (1988), the only neotropical frogs having “ossified” intercalary elements are the hylines *Sphaenorhynchus carneus*, *Aplastodiscus perviridis*, and *Scarthyla ostinodactyla*, and species in the pseudid genera *Lysapsus* and *Pseudis*. We now add to this list some species of *Centrolenella*. Both *C. euhystrix* and *C. hesperia*, as well as one preparation of *C. orientalis* (USNM 257182),

have mineralized intercalary elements. Two preparations of *C. prosoblepon* (USNM 252617–18) did not show mineralized intercalary elements, but these preparations were only lightly stained with alizarin. We suggest that the lack of evidence for mineralization of these intercalary elements may be an artifact.

The histology of the intercalary elements within the family *Centrolenidae* has not been clarified. Noble (1920:443) stated that *Centrolene* possessed “. . . an intercalary bone (or partly ossified cartilage) . . .” but was less clear about the nature of the element in later papers. Although Noble (1925) defined the Hylidae, into which he placed *Centrolene* and *Centrolenella*, as a group having characters of the Bufonidae but with an intercalary cartilage or bone between the ultimate and penultimate phalanges of each digit, he did not state whether the element in the two genera of concern was cartilage or bone. In his monumental work on the biology of the Amphibia, Noble (1931) referred to the Hylidae as bufonids with intercalary cartilages; no mention was made of bony elements. In defining the family *Centrolenidae*, Taylor (1951) listed the trait as intercalary cartilages. All subsequent references to the trait in the *Centrolenidae* have called the structures intercalary cartilages (e.g., Eaton 1958, Duellman 1975, Dowling & Duellman 1978, Duellman 1988) or cartilaginous intercalary elements (Duellman & Trueb 1986). Peters (1964:166) called the structure “intercalary cartilage” and described it as “a phalanx-like cartilaginous (occasionally bony?) element. . . .” Even though one of the other synonyms (intercalary phalanx) listed by Peters (1964) referred to both cartilage or bone intercalated between the normal components of the digit, the use of a question mark suggests to us that Peters was unsure of the nature of the element or confused by previous usage.

Given the prevalence of mineralized intercalary elements among species of *centrolenids* as evidenced by our observations and

those of David C. Cannatella (pers. comm.), we recommend that “mineralized intercalary elements” be recognized as a diagnostic feature of the family *Centrolenidae* (contra Duellman & Trueb 1986, Duellman 1988).

The Monte Seco area.—The western slopes of the Peruvian Andes generally are arid, through local conditions sometimes permit more humid areas, as in the vicinity of Monte Seco. Koepcke (1961) summarized general features of the vegetation and climate of the western Andean slopes of Peru, including the Río Zaña valley. In general, the western slopes of northern Peru receive more moisture than those in central and southern Peru. The Río Zaña lies at the southern edge of a transition along the Andean slope where the vegetation changes to a more mesic type; humidity increases as one moves north from this area (Weberbauer 1936). Cadle (1989) briefly detailed some aspects of climate in the Monte Seco area. Additional observations from the beginning of the rainy season (January 1989) are noted here.

When Cadle arrived in the Monte Seco area on 13 January, little rain had fallen as evidenced by the dry soil and lack of recent herbaceous and epiphytic growth. No rain fell on several days between 13 and 20 January. Thereafter, each day was characterized by steady rains and much cloud cover. Precipitation fell either as relatively heavy rains lasting for one to several hours during the day, usually in the afternoon, or as steady daytime drizzles of varying intensity. Rain occurring at night was usually of limited intensity and duration, with most falling before midnight. Dense daytime fogs as had happened during the beginning of the dry season (Cadle 1989) did not occur during this period.

The slopes above Monte Seco are steep with relatively few permanent streams and many waterfalls. Because of the topography, nocturnal work along certain portions of streams is difficult and even dangerous. The highest waterfall, Chorro Blanco, drops

about 200 m. Many others occur in the study streams (Fig. 2) and vary in height from <1 m to >18 m. During the rainy season, many small temporary streams flow from the hills, and in 1987 some of these lasted into the beginning of the dry season (mid-June) but with greatly reduced flow. In addition to natural streams, local inhabitants have constructed a series of drainage ditches (acequias) along the hillside to channel water for domestic use. Long portions of these ditches extend through forested areas, are well-shaded, and have overhanging vegetation that seemingly could have provided suitable egg-laying sites for *Centrolenella* but none were found. *Centrolenella hesperia* bred along both permanent and temporary streams between 1500 m and 1800 m from the vicinity of the type locality; but *C. euhystrix* was observed only along permanent streams near Cadle's field camp (site 2) and at higher elevations (site 1 and one other nearby site, Fig. 2). Apparently, neither species bred along the drainage ditches. This may reflect differences in substrate quality of the ditches (generally sandy) compared to natural streams (gravelly to rocky), gradient (gradually sloping versus precipitous), or some other unknown variable (e.g., differences in oxygen tension between the ditches and streams). Tadpoles of *Colostethus* sp. were found in the drainage ditches, as well as elsewhere in relatively oxygen-poor, standing water with sandy substrates.

Centrolenella euhystrix and *C. hesperia* were found sympatrically only at the type locality of the latter (Fig. 2). This represented the lowest and highest elevations (1800 m), respectively, at which the two species were observed. Greater elevational overlap in the ranges of the two species probably occurs, but the precipitous nature of the streams precluded adequate exploration of this possibility. Owing to its distinctive call and overt behavior, *C. hesperia* was easily detected and thus appeared to be absent from the sites at 2500 m and above where *C. euhystrix* was observed. Although

individuals of *C. euhystrix* were more cryptic, none were observed during a careful search of several waterfalls below 1800 m and at waterfalls along one other permanent stream at about 1800 m. The only other frog which lays eggs along streams in the Monte Seco area is *Telmatobius* sp., but it most likely lays its eggs in the water. Other frogs in the area use terrestrial sites (*Colostethus* and *Eleutherodactylus*) or carry their eggs (*Gastrotheca*). Tadpoles of *Colostethus* sp. were found in the streams (among other sites) at all elevations where adults and eggs of *Centrolenella* were observed. Tadpoles of *Telmatobius* sp. were found only in the streams above 2500 m where *Centrolenella euhystrix* adults (but no tadpoles) were observed; *Gastrotheca* sp. tadpoles were found in ponds or small pools away from streams but only at higher elevations.

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Literature Cited

- Aichinger, M. 1987. Freilandbeobachtungen zum Fortpflanzungsverhalten von *Hyla brevifrons* Duellman & Crump, 1974.—*Salamandra* 23: 269–276.
- Altig, R. 1970. A key to the tadpoles of the continental United States and Canada.—*Herpetologica* 26:180–207.
- Cadle, J. E. 1989. A new species of *Coniophanes* (Serpentes: Colubridae) from northwestern Peru.—*Herpetologica* 45:411–424.
- Cannatella, D. A. 1980. Two new species of *Centrolenella* from Bolivia (Anura: Centrolenidae).—*Proceedings of the Biological Society of Washington* 93:714–724.
- , & W. E. Duellman. 1982. Two new species of *Centrolenella*, with a brief review of the genus in Peru and Bolivia.—*Herpetologica* 38:380–388.
- , & W. W. Lamar. 1986. Synonymy and distribution of *Centrolenella orientalis* with notes on its life history (Anura: Centrolenidae).—*Journal of Herpetology* 20:307–317.
- Cochran, D. M., & C. J. Goin. 1970. Frogs of Colombia.—*United States National Museum Bulletin* 288:1–605.
- Dingerkus, G., & L. D. Uhler. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage.—*Stain Technology* 52:229–232.
- Dowling, H. G., & W. E. Duellman. 1978. Systematic herpetology: a synopsis of families and higher categories. HISS Publications, New York.
- Drewes, R. C. 1984. A phylogenetic analysis of the Hyperoliidae (Anura): treefrogs of Africa, Madagascar, and the Seychelles Islands.—*Occasional Papers of the California Academy of Sciences*. 139:1–70.
- Duellman, W. E. 1975. On the classification of frogs.—*Occasional Papers on the Museum of Natural History, The University of Kansas* 42:1–14.
- . 1988. Evolutionary relationships of the Amphibia. Pp 1–34 in B. Fritzsche, M. J. Ryan, W. Wilczynski, T. E. Hetherington, & W. Walkowiak, eds., *The evolution of the amphibian auditory system*. John Wiley & Sons, New York.
- , & P. A. Burrowes. 1989. New species of frogs, *Centrolenella*, from the Pacific versant of Ecuador and southern Colombia.—*Occasional Papers of the Museum of Natural History, The University of Kansas* 132:1–14.
- , & R. O. de Sa. 1988. A new genus and species of South American hylid frog with a highly modified tadpole.—*Tropical Zoology* 1:117–136.
- , & A. H. Savitzky. 1976. Aggressive behavior in a centrolenid frog, with comments on territoriality in anurans.—*Herpetologica* 32:401–404.
- , & L. Trueb. 1986. *Biology of amphibians*. McGraw-Hill Book Company, New York, 670 pp.
- Eaton, T. H. 1958. An anatomical study of a neotropical tree frog, *Centrolene prosoblepon* (Salientia: Centrolenidae).—*The University of Kansas Science Bulletin* 39:459–472.
- Flores, G. 1985. A new *Centrolenella* (Anura) from Ecuador, with comments on nuptial pads and prepollical spines in *Centrolenella*.—*Journal of Herpetology* 19:313–320.
- . 1987. A new *Centrolenella* from the Amazonian lowlands of Colombia.—*Journal of Herpetology* 21:185–190.
- , & R. W. McDiarmid. 1989. Two new species of South American *Centrolenella* (Anura: Centrolenidae) related to *C. mariae*.—*Herpetologica* 45:401–411.
- Frost, D. R. (ed.). 1985. *Amphibian species of the world, a taxonomic and geographical reference*. Association of Systematics Collections, Lawrence, Kansas, 732 pp.
- Goin, C. J. 1964. Distribution and synonymy of *Centrolenella fleischmanni* in northern South America.—*Herpetologica* 20:1–8.
- Gosner, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification.—*Herpetologica* 16:183–190.
- Ham, A. W., & D. H. Cormack. 1979. *Histophysiology of cartilage, bone, and joints*. J. B. Lippincott Company, Philadelphia.
- Jacobson, S. K. 1985. Reproductive behavior and male mating success in two species of glass frogs (Centrolenidae).—*Herpetologica* 41:396–404.
- Jungfer, K.-H. 1988. Froschlurche von Fortuna, Panama II. Hylidae (2), Centrolenidae, Dendrobatiidae.—*Herpetofauna* 10(56):6–12.
- Koepcke, H. W. 1961. Synökologische studien an der westseite der peruanischen Anden.—*Bonner Geographische Abhandlungen* 29:1–320.
- Leviton, A. E., R. H. Gibbs, Jr., E. Heal, & C. E.

- Dawson. 1985. Standards in herpetology and ichthyology: part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology.—*Copeia* 1985:802–832.
- Lieb, C. S. 1988. Systematic status of the neotropical snakes *Dendrophidion dendrophis* and *D. nuchalis* (Colubridae).—*Herpetologica* 44:162–175.
- Lynch, J. D. 1969. Taxonomic notes on Ecuadorian frogs (Leptodactylidae: *Eleutherodactylus*).—*Herpetologica* 25:262–274.
- , & W. E. Duellman. 1973. A review of the centrolenid frogs of Ecuador, with descriptions of new species.—*Occasional Papers of the Museum of Natural History, The University of Kansas* 16:1–66.
- , P. M. Ruiz, & J. V. Rueda. 1983. Notes on the distribution and reproductive biology of *Centrolene geckoideum* Jiménez de la Espada in Colombia and Ecuador (Amphibia: Centrolenidae).—*Studies on Neotropical Fauna and Environment* 18:239–243.
- McDiarmid, R. W., & K. Adler. 1974. Notes on territorial and vocal behavior of neotropical frogs of the genus *Centrolenella*.—*Herpetologica* 30:75–78.
- Myers, C. W., & W. E. Duellman. 1982. A new species of *Hyla* from Cerro Colorado, and other tree frog records and geographical notes from western Panama.—*American Museum Novitates* 2752:1–32.
- Noble, G. K. 1920. Two new batrachians from Colombia.—*Bulletin of the American Museum of Natural History* 42:441–446.
- . 1924. Some neotropical batrachians preserved in the United States National Museum with a note on the secondary sexual characters of these and other amphibians.—*Proceedings of the Biological Society of Washington* 37:65–72.
- . 1925. An outline of the relation of ontogeny to phylogeny within the Amphibia. I.—*American Museum Novitates* 165:1–17.
- . 1931. *The Biology of the Amphibia*. McGraw-Hill Book Company, New York. 577 pp.
- , & M. E. Jaekle. 1928. The digital pads of the tree frogs. A study of the phylogenesis of an adaptive structure.—*Journal of Morphology and Physiology* 45:259–292.
- Peters, J. A. 1964. *Dictionary of Herpetology*. Hafner Publishing Company, New York. 392 pp.
- Poole, A. R., Y. Matsui, A. Hinek, & E. R. Lee. 1989. Cartilage macromolecules and the calcification of cartilage matrix.—*The Anatomical Record* 224:167–179.
- Ruiz-Carranza, P. M., J. Hernández-Camacho, & M. C. Ardila-Robayo. 1986. Una nueva especie Colombiana del genero *Centrolene* Jiménez de la Espada 1872 (Amphibia: Anura) y redefinición del genero.—*Caldasia* 15(71–75):431–444.
- Savage, J. M. 1967. A new tree-frog (Centrolenidae) from Costa Rica.—*Copeia* 1967:325–331.
- , & W. R. Heyer. 1967. Variation and distribution in the tree-frog genus *Phyllomedusa* in Costa Rica, Central America.—*Beiträge zur Neotropischen Fauna* 5(2):111–131.
- , & P. H. Starrett. 1967. A new fringe-limbed tree-frog (Family Centrolenidae) from lower Central America.—*Copeia* 1967:604–609.
- Starrett, P. H., & J. M. Savage. 1973. The systematic status and distribution of Costa Rican glass-frogs, genus *Centrolenella* (Family Centrolenidae), with description of a new species.—*Bulletin of the Southern California Academy of Sciences* 72:57–78.
- Taylor, E. H. 1949. Costa Rican frogs of the genera *Centrolene* and *Centrolenella*.—*The University of Kansas Science Bulletin* 33:257–270.
- . 1951. Two new genera and a new family of tropical American frogs.—*Proceedings of the Biological Society of Washington* 64:33–40.
- Weberbauer, A. 1936. *Phytogeography of the Peruvian Andes*.—*Field Museum of Natural History, Botanical Series*, 13. *Flora of Peru, Part 1*: 13–81.

(JEC) Department of Herpetology, Academy of Natural Sciences, 19th and the Parkway, Philadelphia, Pennsylvania 19103; and (RWM), United States Fish and Wildlife Service, Biological Survey, National Museum of Natural History, Washington, D.C. 20560.